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LIFE HISTORY OF THE CANNONBALL JELLYFISH, *STOMOLOPHUS MELEAGRIS* L. AGASSIZ, 1860 (SCYPHOZOA, RHIZOSTOMIDA)

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Abstract

Stages in the life history of the scyphozoan *Stomolophus meleagris* from the planula to the newly liberated ephyra were raised in the laboratory and are described for the first time. After swimming actively for 2–5 days, the ciliated planula larvae settled and scyphistoma morphogenesis occurred. Fully developed scyphistomae were cone-shaped and bore a whorl of about 16 tentacles around a dome- or knob-shaped proboscis. Podocyst formation was the only observed method of asexual reproduction in cultures of scyphistomae maintained for one month. Strobilation began as soon as nine days after scyphistoma morphogenesis and occurred in scyphistomae with as few as eight tentacles. The strobilation process, completed in about 3.5 days at 25°C, was not accompanied by any noteworthy color changes. Most strobilae produced two ephyrae each, although the number varied from one to three. Some scyphistomae began to strobilate a second time within a week after completion of an initial round of strobilation. Newly liberated ephyrae possessed a normal complement of eight lappet pairs and eight rhopalia. They were morphologically similar to, yet distinguishable from, ephyrae of the related species *Rhopilema verrilli*. None of the examined stages of *S. meleagris* contained algal symbionts.

Introduction

Biologists did not recognize the relationship between polyp and medusa stages in the Cnidaria until life history studies were undertaken on scyphozoans by Sars (1829, 1835, 1841), Dalyell (1836), and Siebold (1839). Polypoid and medusoid forms, previously regarded as separate taxa, were both found to occur in the life cycles of *Aurelia aurita* and *Cyanea capillata*. Sars, in the course of his studies, also demonstrated that *Scyphistoma, Strobila*, and *Ephyra* were stages in the life cycle of scyphozoans rather than being separate genera.

In the years since these early studies, complete life histories have been described for few of the 200 known species of Scyphozoa. In the Hydrozoa, such investigations have become frequent to resolve problems of classification and synonymy; separate classification systems for polyps and medusae have been used in the class, and polypoid and medusoid stages of a species have often been known by different names. Comparable problems in scyphozoan systematics have been relatively minor because the conspicuous and relatively divergent species of scyphomedusae have been named and classified while their small, obscure, and morphologically indistinct polyps have not. The one notable exception is the genus *Stephanoscyphus* Allman, 1874, whose polyps are protected by a well-developed sheath of perisarc. Originally thought to be a hydrozoan, *Stephanoscyphus* gives rise to scyphomedusae of the order Coronatae.

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With the dearth of life history investigations in the Scyphozoa, stages other than the medusa are often unknown even for some of the more common species. Strobilation, a process in which the medusoid form is derived from the polypoid form, likewise remains undescribed for most scyphozoans. So it is with *Stomolophus meleagris* L. Agassiz, 1860, one of the most abundant species of scyphomedusae along the southeastern and Gulf coasts of the United States (Mayer, 1910; Kraeuter and Setzler, 1975; Burke, 1976; Calder and Hester, 1978). Various phases in the development of the medusa only have been described in this species (Mayer, 1910; Stiasny, 1922). The purpose of this paper is to describe the life history of *S. meleagris* from planula to newly liberated ephyra stages, including observations on the strobilation process.

Materials and Methods

Stages in the life history of *Stomolophus meleagris* were raised in the laboratory from planula larvae obtained from identified medusae. Planulae were first isolated in cultures on 5 March 1974 from a holding tank containing medusae of *S. meleagris* collected in the Cooper River at Charleston, South Carolina. Scyphistomae were observed in these cultures two days later, but all died within a week. Planulae were obtained a second time from medusae collected 14 July 1981 about 1.5 km offshore from the entrance of Murrells Inlet, South Carolina. A bucket containing one male and one female medusa was placed in a mesh bag and suspended overnight just below the surface of the water. The following morning, water, debris, and planulae from the bottom of the bucket were poured into large preparation dishes. Planulae present in these dishes were isolated in a fingerbowl containing 200 ml of filtered seawater of 35.7‰ salinity. The fingerbowl was covered, and the culture was maintained at room temperature ($\approx$27°C) in the laboratory.

Developing scyphistomae were fed pieces of newly hatched *Artemia* several times a day until they were large enough to ingest entire nauplii. Undigested materials were removed daily from the cultures using a pipette, and the water was changed at least once a week. Strobilation was observed in polyps maintained both at room temperature and at 25°C in a constant temperature cabinet.

Cultures were lost, apparently due to a bacterial infection, one month after being established.

Descriptions

Planula

Planulae, somewhat flattened in cross-section, varied in outline from elongate-cylindrical to slipper-shaped to irregularly oval (Fig. 1a) and measured 120–390 μm long and 60–130 μm wide. The anterior and posterior ends were rounded. They were mouthless, and a solid, inner, endodermal mass was enclosed by an outer, ciliated ectoderm. Living planulae were translucent-whitish in color.

Scyphistoma

At metamorphosis, planulae attached by the anterior end to the substrate and gradually became flask-shaped as the narrowing stalk of the developing scyphistoma differentiated from the expanding calyx. Newly metamorphosed scyphistomae (Figs. 1b,c) varied from 200–430 μm in height from pedal disk to mouth. A thin cuticle enveloped the slender stalk. Tentacles, usually four in number but sometimes

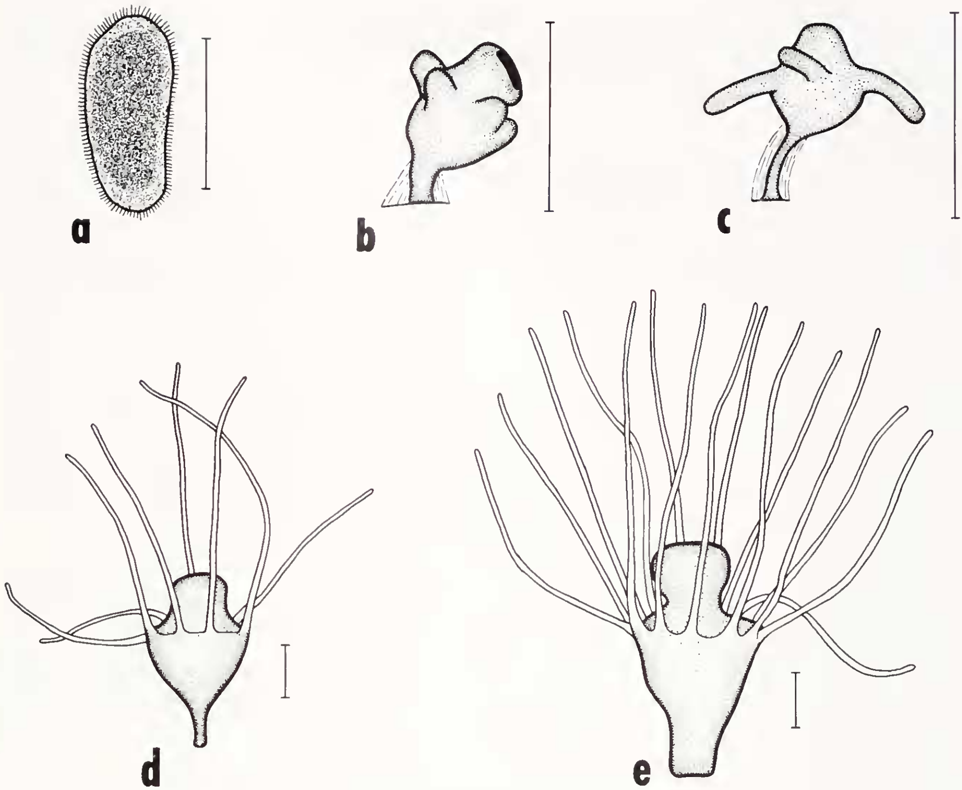

FIGURE 1. Planula and scyphistoma stages of *Stomolophus meleagris*. a. Planula. b. Newly metamorphosed scyphistoma. c. Young scyphistoma. d. Intermediate, 8-tentacled scyphistoma. e. Fully developed scyphistoma. Scale bars = 250 μm.

as few as two and as many as six, appeared near the distal end of the bulbous calyx. They were filiform with scattered nematocyst batteries, and occurred in one whorl. The oral disk was largely occupied by a prominent, dome-shaped proboscis. The mouth, round or irregular in shape, was capable of considerable dilation. The color was translucent-whitish.

Intermediate scyphistomae (Fig. 1d) were 0.5–1.0 mm high and bore eight very contractile tentacles. These were filiform with scattered nematocyst batteries, and occurred in one whorl. The stalk was slender, and the cuticle originally enclosing the stalk had become vestigial. The calyx was cone-shaped. A large, flexible, dome-shaped proboscis occupied most of the oral disk, which bore four peristomial pits. The expansible mouth was round, irregular, or quadrate, and the pharynx was quadrate. The color was translucent-whitish, but the endoderm became light orange after digestion of *Artemia*.

Fully developed scyphistomae (Fig. 1e) attained about 2 mm in height from pedal disk to mouth and bore about 16 filiform tentacles. Tentacles were contractile, in one whorl, and had scattered nematocyst batteries. The moderately thick stalk was somewhat variable in length and merged almost imperceptibly with the cone-shaped calyx. The proboscis was large, flexible, and dome- or knob-shaped. The mouth continued to be expansible, and was round, irregular, or quadrate in shape.

The pharynx was quadrate, and the oral disk bore four prominent peristomial pits. The color was whitish, with the endoderm becoming light orange after digestion of *Artemia.*

Strobila

Elongation of the calyx occurred in the early strobila, but the first clear external indication of strobilation was the development of a small marginal lobe at the base of each rhopalar tentacle (Fig. 2a). About six hours later, segmentation began as a faint circular incision proximal to the tentacular ring; this incision became progressively deeper and more pronounced (Fig. 2b). A second or even a third incision

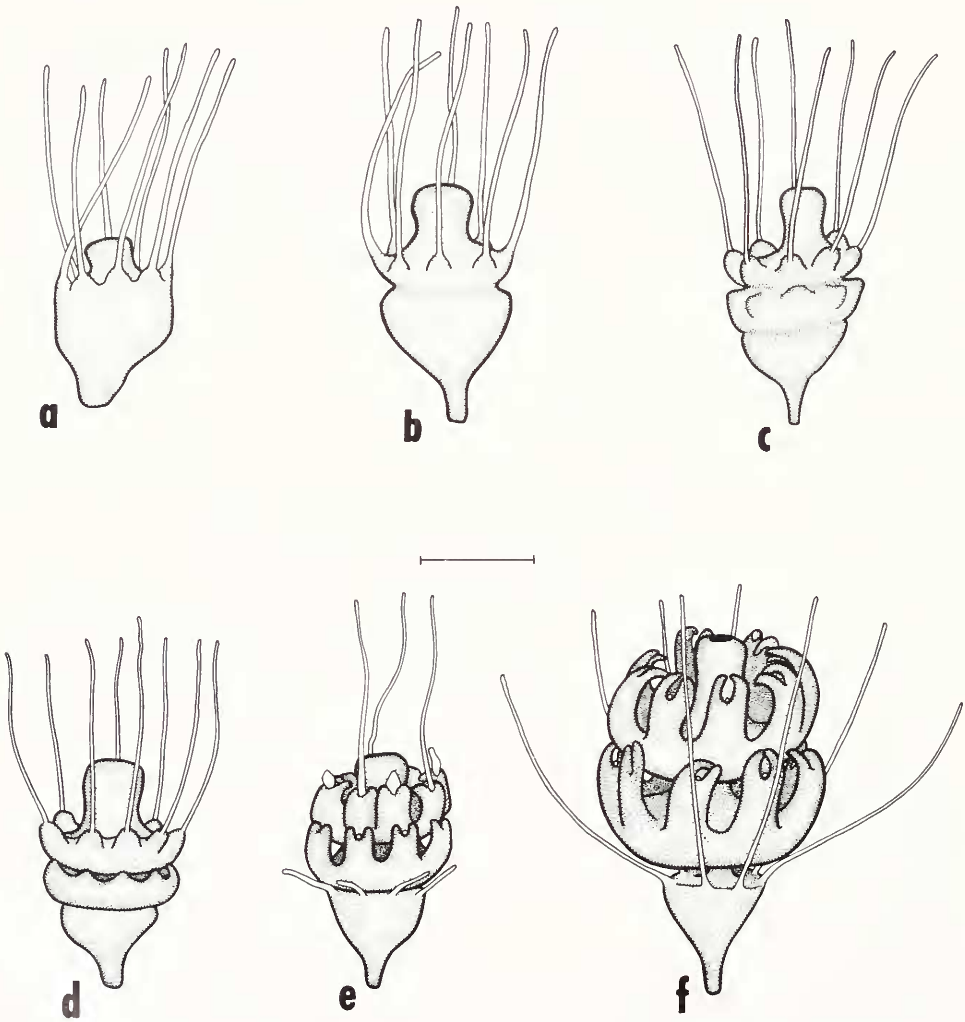

FIGURE 2. Strobilae of *Stomolophus meleagris.* a. Early strobila with tentacular lobes. b. Early strobila with incision. c. Early strobila with second incision. d. Early strobila with developing segments. e. Mid-strobila, with regressing tentacles and developing ephyral segments. f. Late strobila with well developed ephyra segments and basal polyp. Scale bar = 500 μm.

subsequently appeared proximal to the first in polydisk strobilae, each forming a segment representing an incipient ephyra (Fig. 2c). As strobilation proceeded, the proboscis became enlarged, tentacular lobes on the distal segment became more pronounced, and marginal lobes became progressively better defined about the periphery of any proximal segments (Figs. 2c,d).

About 36 hours into the strobilation process, tentacles began to undergo regression, contracting and expanding periodically. The eight rhopalar tentacles were resorbed, some more rapidly than others (Fig. 2e), into the cleft between the developing lappets on each marginal lobe. If tentacles in addition to the eight rhopalar ones were present, they were resorbed into the ocular clefts between the marginal lobes. Simultaneous with tentacular regression, rhopalia with statoliths became apparent, lappets elongated, incisions constricting the segments deepened, manubrium development progressed on any proximal ephyral segments, a new proboscis began to form on the basal polyp, and the polyp began to regenerate new tentacles. Nascent ephyrae, beginning with the one at the distal end, became capable of contractions. These movements were weak at first, but became progressively stronger and more frequent. Tentacles of the original scyphistoma were completely resorbed about 54 hours into strobilation.

In the late strobila (Fig. 2f), incisions continued to deepen and separate the developing ephyrae. Ephyrae increased markedly in size and underwent rapid development prior to release. Pulsations became stronger and occurred more frequently. Development of the manubria in proximal ephyrae and proboscis in the polyp proceeded. Gastric cirri were visible in the developing ephyra prior to liberation. Ephyrae were liberated about 3.5 days after strobilation began.

Ephyra

Newly liberated ephyrae (Figs. 3a,b) were about 1.5–2.0 mm wide from lappet-tip to lappet-tip. There were typically eight marginal lobes, eight rhopalia, and eight pairs of slender, distally pointed lappets. Rhopalar clefts were U-shaped and slightly more than half as deep as the large ocular clefts separating the marginal lobes. The manubrium was small and cruciform in cross-section. Four lips were often present about the mouth, but oral arms were lacking and no papillae were present. The stomach portion of the gastrovascular cavity was nearly circular, and 1–2 gastric cirri were present in each quadrant. Eight blunt-ended rhopalar canals and eight small adradial bulges extended peripherally from the central stomach. Coronal muscles were barely evident in unstained specimens, but the radial muscles were visible extending to each lappet from the marginal lobes. The exumbrella was marked by a ring of small nematocyst batteries about the periphery of the stomach, and a large, elongate battery was present on each marginal lobe. The mesoglea was thin. The ectoderm was pale straw colored, while the remainder of the ephyra was translucent.

General Observations

Planula larvae of *S. meleagris* are apparently not incubated by the adult medusae. Medusae of both sexes were dissected and examined microscopically for incubated planulae during studies in 1974 and 1981, but none were found. Planulae obtained both years were found free in containers of water in which sexually mature medusae had been held overnight.

Planulae swam actively by ciliary propulsion, rotating counterclockwise around the anterior-posterior axis. Within two to five days they attached by the anterior

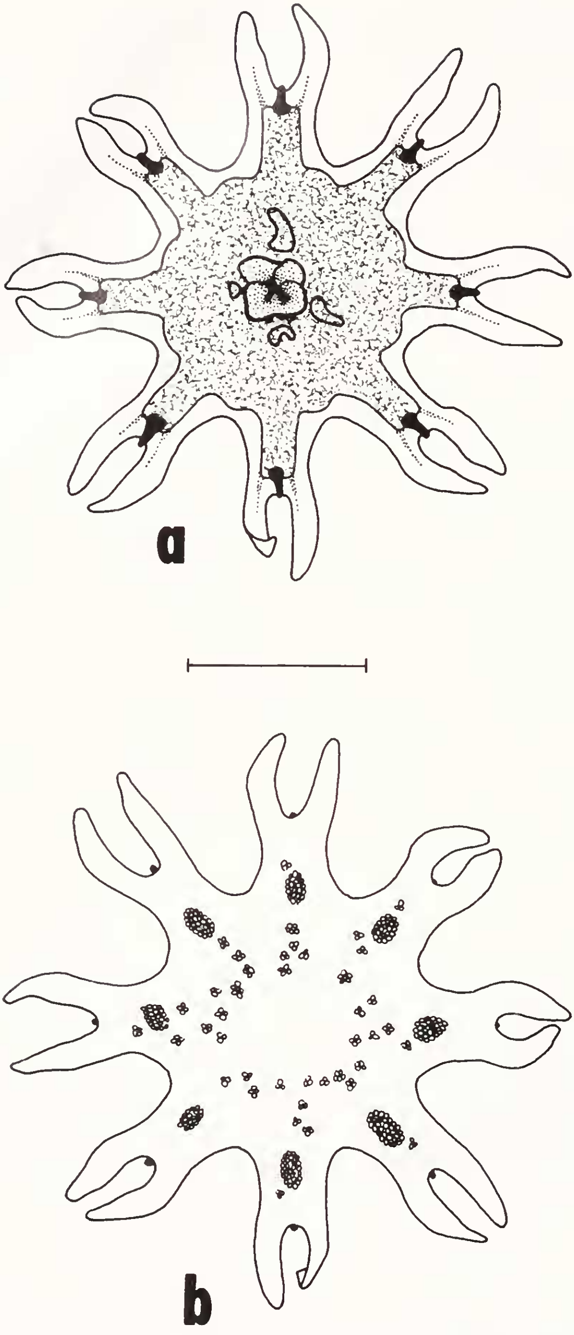

FIGURE 3. Newly liberated ephyra of *Stomolophus meleagris.* a. Subumbrellar view. b. Exumbrellar view. Scale bar = 500 μm.

end and metamorphosed directly into scyphistomae, without an intervening larval cyst stage.

Recently metamorphosed scyphistomae were sessile, but if dislodged were capable of slow locomotion along the bottom of the container using the cilia. Dislodged polyps eventually reattached through the formation of a pedal stolon, which became anchored to the substrate. Little is known about asexual reproduction in the polyp of *S. meleagris*. However, one scyphistoma with 16 tentacles was forming a podocyst shortly before loss of the culture.

Strobilae were first observed in the cultures only nine days after polyp morphogenesis occurred. Scyphistomae as small as 1 mm or less, and bearing as few as eight tentacles, became strobilae. The strobilation process was neither preceded nor accompanied by any noteworthy changes from the translucent, pale straw color assumed by the developing ephyrae. In most cases, two ephyrae were formed by each strobila, although as few as one and as many as three were produced on occasion. Some of the scyphistomae of *S. meleagris* strobilated a second time, as soon as a week after completion of the initial strobilation.

Ephyrae produced during strobilation swam actively and appeared to be normal morphologically. No attempt was made to raise the ephyrae, and most were preserved shortly after liberation.

None of the life stages of *S. meleagris* examined during this study bore algal symbionts.

Discussion

Agassiz (1860, 1862) described and illustrated the medusa of *Stomolophus meleagris* from specimens collected at Wassaw Island, Georgia, and Charleston, South Carolina. The species has subsequently been reported from New England to Brazil in the western Atlantic (Kramp, 1961; Larson, 1976), but its occurrence north of Cape Hatteras is probably due largely or entirely to transport in water currents. Elsewhere, it has been recorded from southern California to Ecuador in the eastern Pacific and from the Sea of Japan to the South China Sea in the western Pacific (Kramp, 1961; Omori, 1978). In the orient, *S. meleagris* is one of several rhizostome medusae used for human consumption (Omori, 1978, 1981).

Medusae of *S. meleagris* are frequent in coastal waters from North Carolina to Florida and in the northern Gulf of Mexico (Mayer, 1910). Kraeuter and Setzler (1975) reported finding medusae of this species from March through October in Georgia, and Burke (1976) noted that *S. meleagris* was almost always present in Mississippi Sound. In South Carolina, they occur sporadically throughout the year and at times are a hinderance to commercial shrimp trawling because of their abundance (Calder and Hester, 1978). As with many species of scyphomedusae, abundances vary greatly from year to year as well as from season to season. Despite their frequency of occurrence in waters of the southeast and Gulf coasts of the United States, medusae of this species are an insignificant public health hazard because the toxin of their nematocysts is relatively innocuous to humans (Toom and Chan, 1972).

The life history of *S. meleagris* (Fig. 4) resembles that described for other species of neritic Scyphozoa (Naumov, 1961; Russell, 1970). The fertilized egg develops into a tiny, motile planula larva. After swimming freely in the water for several days, the planula attaches to a suitable substrate and transforms into a sessile polyp or scyphistoma. Scyphistomae feed and grow, attaining a maximum size of a few millimeters. They reproduce asexually a number of ways, including the formation of podocysts and motile or non-motile buds, but only podocyst formation was observed in *S. meleagris*. In addition to their function in asexual reproduction, podocysts in the Scyphozoa are resistant to adverse environmental conditions (Cargo and Schultz, 1966). Under favorable conditions the scyphistoma

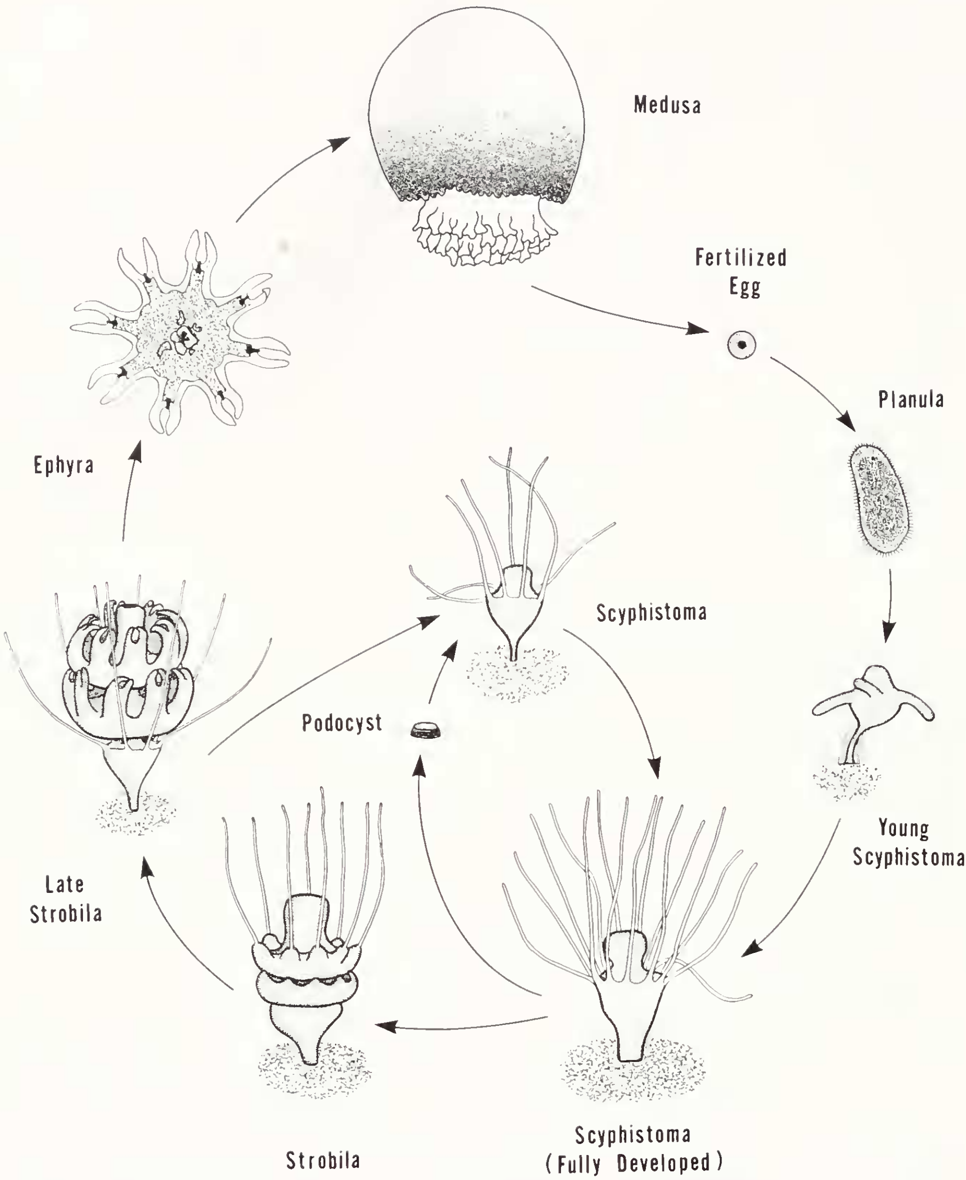

FIGURE 4. General life history of the scyphozoan *Stomolophus meleagris*. See text for explanation.

undergoes strobilation; during this process the polyp is known as a strobila. Two separate developmental phenomena, namely segmentation and metamorphosis, are involved in the strobilation process (Thiel, 1938; Spangenberg, 1968). Strobilation results in the derivation of several organisms from a single individual. One or more free-swimming ephyrae may be produced, and the basal portion of the strobila is left as a small scyphistoma after release of the ephyrae. This small scyphistoma rapidly returns to normal size and is capable of repeated strobilation. Ephyrae develop into medusae, completing the life cycle.

Scyphopolyps have been described for relatively few species of Scyphozoa. Known polyps of the order Coronatae are distinctive in being elongate forms enveloped in a chitinous tube (Russell, 1970). They resemble, and were believed by Chapman (1966) and Werner (1966, 1967a,b, 1970, 1973) to be related to, the fossil Conulata. Chapman (1973) observed behavioral as well as morphological differences between coronate and semaeostome polyps. Semaeostome and rhizostome scyphistomae display considerable morphological similarity from species to species within and between orders. The basic form is that of a goblet or cone, attached aborally by a pedal disk, and bearing an oral whorl of tentacles (Russell, 1970). A cuticular theca, if present at all, is vestigial (Chapman, 1966, 1968).

Among the rhizostomes, scyphistomae are known for *Cassiopea andromeda, Cephea cephea, Cotylorhiza tuberculata, Mastigias papua, Rhizostoma pulmo, Rhopilema verrilli*, and now *Stomolophus meleagris* (Table I). Of these, *S. meleagris* most closely resembles *R. verrilli* in its cone-shaped calyx and long proboscis. The only reliable way to distinguish polyps of these two species at present would be to induce and observe strobilation. Red and orange pigments appear during strobilation in the developing ephyrae of *R. verrilli* that are lacking in *S. meleagris*. Studies on the nematocysts of scyphistomae and other stages of *S. meleagris*, underway as part of another investigation, may provide a means of separating the two species. Diagnostic differences in the nematocyst complement were detected in scyphistomae of the semaeostomes *Aurelia aurita, Chrysaora quinquecirrha*, and *Cyanea capillata* (Calder, 1971).

Scyphistomae of *S. meleagris* began to strobilate prior to attaining full development. Polyps as young as nine days old, measuring 1 mm or less in height and bearing as few as eight tentacles, were observed undergoing strobilation. Ephyrae produced by these strobilae appeared normal in all respects. Strobilation so soon after scyphistoma morphogenesis was unexpected but may not be unusual in the Scyphozoa, given optimal conditions. Strobilation has also been observed, under field conditions, in polyps of *Chrysaora quinquecirrha* that were less than two weeks old (D. G. Cargo, Chesapeake Biological Laboratory, personal communication).

Strobilation in the Scyphozoa may be monodisk, in which one ephyra is produced, or polydisk, in which two or more ephyrae are produced. Although monodisk strobilation appears to be common in the rhizostomes (Table I), it can no longer be regarded as a fixed characteristic of the group, as suggested by Sugiura (1966). Polydisk strobilation was the norm in *S. meleagris*, and has been observed in three other species of rhizostomes (Table I). Conversely, Uchida and Sugiura (1978) demonstrated that strobilation in the semaeostome *Sanderia malayensis* was monodisk. Strobilation in semaeostomes such as *Cyanea capillata, Aurelia aurita*, and *Chrysaora quinquecirrha* is usually, but not always, of the polydisk type (Berrill, 1949; Spangenberg, 1968; Calder, 1974). Berrill (1949) concluded that the type of strobilation depended upon the size and shape of the scyphistoma. Monodisk strobilation usually occurs in polyps having a short calyx, while polydisk strobilation normally occurs in polyps having an elongate, columnar calyx. The type of strobilation thus appears to have little or no phylogenetic significance within the Scyphozoa.

Several polyps underwent strobilation twice during the month that cultures of *S. meleagris* were maintained in the laboratory. However, strobilation several times in succession is well known in the Scyphozoa, having been reported in species such as *Chrysaora quinquecirrha* (Cargo and Schultz, 1967; Loeb, 1972; Calder, 1974; Cargo and Rabenold, 1980), *Aurelia aurita* (Thiel, 1962), *Cassiopea andromeda*

TABLE I

A summary of some attributes of seven known species of rhizostome polyps.

Species	Shape	No. tentacles	Color	Algal symbionts	Asexual reproduction	Strobilation	Strobila color	References
Cassiopea andromeda (Forskål, 1775)*	goblet-shaped, stalk long, oral disk wide	32±	greenish brown	present (sometimes absent in young scyphistomae)	motile buds	monodisk (infrequently polydisk)	greenish brown	Bigelow (1900) Gohar & Eisawy (1960b) Ludwig (1969) Neumann (1977, 1979) Hofmann, *et al.* (1978) Neumann, *et al.* (1980) Rahat & Adar (1980)
Cephea cephea (Forskål, 1775)	goblet-shaped, stalk long, oral disk width moderate	16	white	absent	motile buds	monodisk	yellow, yellowish brown	Sugiura (1966)
Cotylorhiza tuberculata (Macri, 1778)	goblet-shaped, stalk long, oral disk width moderate	16		present	motile buds	monodisk		Claus (1890, 1893)
Mastigias papua (Lesson, 1830)	goblet-shaped, stalk long, oral disk width moderate	16	white	absent (zooxanthellae could be introduced)	motile buds	monodisk	yellow-green	Uchida (1926) Sugiura (1963)

TABLE I—*Continued*

Species	Shape	No. tentacles	Color	Algal symbionts	Asexual reproduction	Strobilation	Strobila color	References
Rhizostoma pulmo (Macri, 1778)	cone-shaped, stalk length moderate, oral disk wide	32		absent	motile buds, polyp buds, stolon buds, podocysts, strobila buds	polydisk		Paspaleff (1938)
Rhopilema verrilli (Fewkes, 1887)	cone-shaped, stalk length moderate, oral disk width moderate, proboscis clavate	16+	whitish	absent	podocysts	monodisk (occasionally polydisk)	whitish, developing ephyrae with red and orange pigments	Cargo (1971) Calder (1973)
Stomolophus meleagris L. Agassiz, 1860	cone-shaped, stalk length moderate, oral disk width moderate, proboscis dome- or knob-shaped	16	whitish	absent	podocysts	polydisk (occasionally monodisk)	whitish	

* Gohar and Eisawy (1960a) and Neumann (1979) have been followed in regarding *Cassiopea xamachana* Bigelow, 1892 as a synonym of *C. andromeda* (Forskål, 1775).

(Gohar and Eisawy, 1960a), *Mastigias papua* (Sugiura, 1963), and *Cephea cephea* (Sugiura, 1966).

The ephyra is the least differentiated and most difficult stage to identify in the development of the medusa of scyphozoans. Russell (1970) distinguished ephyrae of *Aurelia aurita, Chrysaora hysoscella, Cyanea* spp., and *Rhizostoma octopus* from Britain using morphological differences in radial canal shape, number of gastric filaments, marginal tentacle development, and arrangement of nematocyst batteries on the exumbrella. Ephyrae of *Aurelia aurita, Chrysaora quinquecirrha, Cyanea capillata*, and *Rhopilema verrilli* from the east coast of the United States have been distinguished on the basis of morphology (Larson, 1976) and nematocyst complement (Calder, 1977). Of these four species, newly liberated ephyrae of *S. meleagris* most closely resemble *R. verrilli*. Unlike *R. verrilli*, they have (1) faint instead of prominent adradial bulges in the gastrovascular cavity; (2) a small manubrium with no papillae; (3) no rose or orange pigments in the stomach and manubrium endoderm; (4) a different arrangement of nematocyst batteries on the exumbrella. Ephyrae of *S. meleagris* were also smaller at liberation than those of *R. verrilli* described by Calder (1973), but this may have been due in part to the small size of the strobilae.

Acknowledgments

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